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Genetic analysis of maize shank length by QTL mapping in three recombinant inbred line populations

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ABSTRACT

In maize, the shank is a unique tissue linking the stem to the ear. Shank length (SL) mainly affects the transport of photosynthetic products to the ear and the dehydration of kernels via regulated husk morphology. The limited studies on SL revealed it is a highly heritable quantitative trait controlled by significant additive and additive-dominance effects. However, the genetic basis of SL remains unclear. In this study, we analyzed three maize recombinant inbred line (RIL) populations to elucidate the molecular mechanism underlying the SL. The data indicated the SL varied among the three RIL populations and was highly heritable. Additionally, the SL was positively correlated with the husk length (HL), husk number (HN), ear length (EL), and ear weight (EW) in the BY815/K22 (BYK) and CI7/K22 (CIK) RIL populations, but was negatively correlated with the husk width (HW) in the BYK RIL population. Moreover, 10 quantitative trait loci (QTL) for SL were identified in the three RIL populations, five of which were large-effect QTL. The percentage of the total phenotypic variation explained by the QTL for SL was 13.67 %, 20.45 %, and 30.81 % in the BY815/DE3 (BYD), BYK, and CIK RIL populations, respectively. Further analyses uncovered some genetic overlap between SL and EL, SL and ear row number (ERN), SL and cob weight (CW), and SL and HN. Unlike the large-effect QTL qSL BYK-2−2, which spanned the centromere, the other four large-effect QTL were delimited to a single peak bin via bin map. Furthermore, 2, 5, 6, and 12 genes associated with SL were identified for qSL BYK-2−1, qSL CIK-2−1, qSL CIK-9−1, and qSL CIK-9−2, respectively. Five of the candidate genes for SL may contribute to the hormone metabolism and sphingolipid biosynthesis regulating cell elongation, division, differentiation, and expansion. These results may be relevant for future studies on the genetic basis of SL and for the molecular breeding of maize based on marker-assisted selection to develop new varieties with an ideal SL.

1. Introduction

Maize production in China mainly relies on small-scale farming involving family owned and operated farms, resulting in increased overall costs. Thus, intensive production may be better for the large-scale cultivation of maize. Mechanized harvesting can substantially decrease production costs, but it is most appropriate for grains that have a high dehydration rate. In maize plants, the shank supporting the ear is a unique channel that transports photosynthetic products to the ear [1]. Previous studies revealed that the shank length (SL) has two main effects. Specifically, correlation analyses proved that SL can influence yield [2–4]. Additionally, the husk grows directly on the shank, so SL indirectly affects the grain dehydration rate via husk traits [5,6]. Therefore, clarifying the genetic mechanism underlying SL may generate useful information for cultivating high-yielding maize varieties with grains that dehydrate relatively rapidly, making them suitable for

Abbreviations: SL, shank length; HL, husk length; HN, husk number; HW, husk width; EL, ear length; CW, cob weight; EW, ear weight; ERN, ear row number; PH, plant height; EH, ear height; BJ, Beijing; LN, Liaoning; NM, Neimeng; RIL, recombinant inbred line; BLUP, best linear unbiased prediction; QTL, quantitative trait locus; SNP, single nucleotide polymorphisms; JA, jasmonic acid.

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mechanical harvesting.

Although several studies have examined the maize shank in terms of physiology and genetics, the genetic basis of SL remains unclear. Studies regarding shank development proved that the photosynthates from the leaves and husks are transported to the ear through the shank vasculature, thereby influencing the grain yield [7]. Hansen [8] described SL as a quantitative trait with a narrow heritability of 72.2 % in F_2 populations. Ji et al. [9] developed maize F_2 populations from inbred lines with long and short shanks and observed that SL is associated with a transgressive inheritance phenomenon, with an extremely significant additive effect and a significant additive-dominance effect. A recent study proved that the deletion of two jasmonic acid (JA)-related genes leads to a considerable elongation of the maize shank [10], implying that JA influences SL.

Quantitative trait locus (QTL) mapping is a classical method for identifying QTL in segregating plant populations, including recombinant inbred line (RIL) populations, backcross populations, and doubled haploid populations [11]. The shank is a metamorphic stem, and its morphology and structure are similar to those of the stem. Thus, the results of QTL mapping studies on plant height (PH) may be relevant for mapping QTL related to SL. The QTL for PH and several loci and genes affecting PH in maize have been identified. The QTL for PH are distributed on chromosomes 1–10, and the phenotypic variation explained by a single QTL reportedly ranges from 4.45 % to 22.2 % [12–16]. Some of the PH-related genes are involved in the synthesis, transport, and signaling pathways of hormones that affect PH by modulating internode elongation [17–19], whereas other genes regulate PH via other pathways that directly affect cell division and elongation [20]. Candidate QTL regions defined with the traditional 1-LOD support interval method are too large to identify the related genes [21]. A bin map is a genetic linkage map constructed with bins comprising non-recombinant single nucleotide polymorphisms (SNPs) as markers [22]. Bin maps, which can narrow the QTL interval to the peak bin to identify candidate genes, have been applied to fine map yield-associated loci in sorghum, rice, and maize as well as root-associated loci in maize [23–27]. For example, Li et al. [28] used an $F_{2:3}$ population consisting of 225 lines to map QTL for maize PH and ear height (EH), and identified a common QTL for PH and EH, qPH/EH1-−1, in bin 1.05. The phenotypic evaluation of a near isogenic line population confirmed that this bin can significantly increase PH and EH. Zhang et al. [29] identified a QTL for dry weight on chromosome 7 in a RIL population containing 167 recombinant individuals. The QTL interval was narrowed to the peak bin (161.95–162.04 Mb) before *GRMZM2G057023*, which encodes an interferon-related developmental regulator, was identified as the most likely candidate gene affecting dry weight.

In this study, we analyzed the SL of three RIL populations in different environments and then identified the QTL for SL based on composite interval mapping. We subsequently delimited the large-effect QTL intervals with the bin map and pinpointed the candidate genes affecting the maize SL.

2. Materials and methods

2.1. Plant materials and phenotyping

Three F_6 RIL populations (BY815/DE3, BYD, 207 lines; BY815/K22, BYK, 207 lines; CI7/K22, CIK, 196 lines) and their parents were examined in the present study [30]. These three RIL populations were characterized in an earlier study [31]. All field experiments were conducted according to a randomized complete block design with two block replicates. The three RIL populations and their parents were grown in Beijing (BJ, 40°08′N, 116°10′E), Neimeng (NM, 40°31′N, 107°05′E), and Liaoning (LN, 40°82′N, 123°56′E). Each line was grown in a single-row plot with a row length of 250 cm and 60 cm between rows under natural field conditions. At maturity, six plants were collected per block replicate in each environment, after which the SL (i.e., length from the bottom of the ear to the stem attachment point) was measured with band tapes.

2.2. Statistical and correlation analysis

Data were analyzed with the R software (www.R-project.org). The "aov" function (ANOVA) in the R software was used for the statistical analysis of SL in three environments. The mixed model for the variance analysis was as follows:

$$y_{ijk} = \mu + e_i + r(e)_{ij} + f_k + (f \times e)_{ik} + \varepsilon_{ijk}$$

where μ is the grand mean of SL, e_i is the environmental effect of the *i*th environment, $r(e)_{ij}$ is the effect of the *j*th replication within the *i*th environment, f_k is the genotypic effect of the *k*th line, $(f \times e)_{ik}$ is the effect of the interaction between genetic and environmental effects, and ε_{ijk} is the residual error. All of the variance components in the mixed model were used to calculate the broad-sense heritability with the following equation [32]:

$$h^2 = \sigma_g^2 \Big/ (\sigma_g^2 + \sigma_e^2 \Big/ re + \sigma_{ge}^2 \Big/ e)$$

where σ_g^2, σ_e^2, and σ_{ge}^2 represent the genetic variance, the residual variance, and the genotype and environment interaction variance, respectively, whereas *e* and *r* are the number of environments and replications, respectively.

The best linear unbiased prediction (BLUP) for SL was estimated with the following linear mixed model in the lme4 package of the R software:

$$y_i = \mu + f_i + e_i + \varepsilon_i$$

where y_i is the BLUP value of individual *i*, μ is the grand mean for all environments, f_i and e_i are the *i*th genetic effect and environment effect, respectively, and ε_i is the random error. Additionally, μ was considered to be a fixed effect, whereas f_i and e_i were random effects.

2.3. Genotyping and constructing the bin and genetic linkage maps

Genomic DNA was extracted from the leaf tissue of the three RIL populations and their parents according to the CTAB method and genotyped with the Illumina MaizeSNP50 BeadChip (Illumina Inc., San Diego, CA, USA) containing 56,110 SNPs [33]. The genotyping quality of each SNP was first assessed based on the missing rate, minor allele frequency, and heterozygosity, and each line was also checked regarding the missing rate and heterozygosity with the PLINK software [34]. Following the quality control step, the remaining polymorphic SNPs between the two parental lines were used to construct the genetic linkage map with an economic go-wrong method integrating the CarthaGene software [35]. The continuous polymorphic SNPs with identical genotypes were merged into a bin, which was considered as marker to constructing the bin map. The specific details regarding the construction of the bin and genetic linkage maps were described previously [36].

2.4. QTL mapping

The QTL for SL were analyzed by composite interval mapping [37] with the Zmapqtl program (model 6) in the Windows QTL Cartographer 2.5 software [38]. The scanning interval and window size were set to 0.5 cM and 10 cM, respectively. A forward-backward stepwise regression with five markers controlled the background from flanking markers. The logarithm of the odds (LOD) threshold was estimated by the 1000-permutation test for SL and used to identify the significant QTL ($P \leq 0.05$) [39]. The confidence interval of the QTL position was estimated with the 1-LOD support interval method [40]. The QTL explaining more than 10 % of the phenotypic variance were designated as large-effect QTL, and the remaining QTL were defined as small-effect

QTL [41]. Additionally, QTL detected in at least two environments were stable. Multiple-interval mapping was performed using the Bayesian Information Criteria [42] to determine the interactions between the identified QTL and their total phenotypic variation with the Windows QTL Cartographer 2.5 software.

2.5. Annotation of candidate genes

The large-effect QTL intervals were minimized to a single peak bin interval according to the bin map. The genes within the peak bin interval were screened using the information in the MaizeGDB database (AGPv2). Protein-coding genes were prepared for functionally annotated, and whereas the genes of unknown function or unique to maize were considered designated as unknown. The genes were functionally annotated based on the information regarding homologous Arabidopsis thaliana and rice genes. Genes with homologs related to cell elongation, division, and differentiation were designated as candidate genes for SL.

3. Results

3.1. Phenotypic variation and heritability of maize SL

In this study, t-tests were performed to determine whether there were any significant differences in the SL between the parents of each RIL population. Significant differences were detected between the parents for the BYD and BYK RIL populations (Table 1). Analyses of the BLUP values revealed that the mean SL was close to the mid-parent value in the three RIL populations (Table 1). A normal distribution slightly skewed to the left was observed for the SL in the three RIL populations, which is consistent with the trend of quantitative traits (Fig. 1). The effects of the genotype, environment, and genotype × environment (G × E) interactions on SL were highly significant ($P < 0.01$) in the three RIL populations, with the exception of the environment in the BYK RIL population and G × E in the CIK RIL population (Table 1). Additionally, the high heritability of SL in the three RIL populations indicated by the estimated broad-sense heritability ($h^2_{BYD} = 0.72$, $h^2_{BYK} = 0.79$, and $h^2_{CIK} = 0.72$) (Table 1) implied that the variation in SL was mainly genetically determined. Thus, further QTL mapping was warranted.

3.2. Analysis of the correlation between SL and ear and husk traits in maize

As an important part of the maize ear, the shank affects the grain yield and influences the kernel dehydration rate to some extent, likely because of the interaction between SL and the ear and husk traits. Accordingly, we evaluated the correlation between SL and four ear traits (ear length, EL; cob weight, CW; ear weight, EW; and ear row number, ERN) and three husk traits (husk length, HL; husk width, HW; and husk number, HN) based on Pearson's correlation coefficient. The data for the ear and husk traits were obtained from previous studies [31,43]. Regarding the ear traits, SL was highly positively correlated with EL and EW in the BYK and CIK RIL populations. For the husk traits, with the exception of HN in the BYD RIL population, SL was highly positively correlated with HL and HN in three RIL populations. However, SL was negatively correlated with HW, but only in the BYK RIL population (Fig. 2).

3.3. Analysis of QTL for SL

To minimize the effects of environmental variations, phenotypic BLUP values across three environments were used for QTL mapping. A total of three, three, and four QTL related to SL were detected in the BYD, BYK, and CIK RIL populations, with an empirical threshold LOD value of 3.4, 3.5, and 3.4 after 1000 permutations, respectively (Table 2, Fig. 3). These QTL were located on chromosomes 1, 2, 4, and 9. The average QTL interval was 10.47 Mb (range: 0.9–55.5 Mb). The total phenotypic variation explained by the QTL for SL was 13.67 %, 20.45 %, and 30.81 % in the BYD, BYK, and CIK RIL populations, respectively (Table 2). The phenotypic variation explained by individual QTL in the three RIL populations ranged from 6.15 % (qSL BYD-1−1) to 16.7 % (qSL BYK-2−1). Additionally, qSL BYK-2−1, qSL BYK-2−2, qSL CIK-2−1, qSL CIK-9−1, and qSL CIK-9−2, which explained more than 10 % of the SL variation, were defined as large-effect QTL. The alleles for increasing SL were contributed by the male parent (BY815 for BYD, BY815 for BYK and CI7 for CIK) at all QTL, except for qSL CIK-9−1 and qSL CIK-9−2. Therefore, SL may be controlled by three small-effect QTL in the BYD RIL population, two large-effect QTL and one small-effect QTL in the BYK RIL population, and three large-effect QTL and one small-effect QTL in the CIK RIL population.

To verify the 10 QTL for SL identified based on BLUP values, we also mapped the QTL for SL in different environments (i.e., BJ, LN, and NM) (Fig. S1). The association with SL was stable for qSL CIK-1−1 in BJ, qSL BYK-2−2, qSL CIK-2−1, and qSL CIK-9−2 in LN, qSL BYK-4−1 in BJ and LN, and qSL BYK-2−1 and qSL CIK-9−1 in NM and LN.

3.4. Identification of candidate genes for SL with the bin map

The large-effect QTL associated with SL were narrowed by bin map. Because qSL BYK-2−2 spanned the chromosome 2 centromere region, in which recombinations were rare, we did not identify the genes in this QTL interval (Fig. S2). Regarding the other four large-effect QTL (qSL BYK-2−1, qSL CIK-2−1, qSL CIK-9−1, and qSL CIK-9−2), the intervals

Table 1
Phenotypic performance, variance, and broad-sense heritability of shank length in three RIL populations.

Trait [a]	Populations					
	BYD		BYK		CIK	
Parents						
means ± SD(cm)	BY815	5.95 ± 1.28	BY815	4.25 ± 1.24	CI7	9.70 ± 2.80
	DE3	13.18 ± 2.53	K22	12.2 ± 3.35	K22	11.08 ± 2.51
P value [b]		0.00006		0.0001		0.2598
RILs						
means ± SD(cm)		10.28 ± 2.28		8.45 ± 1.86		9.88 ± 1.72
Range(cm)		5.71−19.18		4.00−14.66		6.28−15.75
F value E [c]		1771.25**		7.59*		469.04**
F value G [d]		5.63**		25.17**		26.07**
F value G × E		1.35**		4.08**		5.67
Heritability [e]		0.72		0.79		0.72

[a] SL, shank length.
[b] P value based on a *t*-test evaluating two parental lines.
[c, d] G and E represent the genotype and environment, respectively, and G × E represents the interaction between G and E.
[e] Family mean-based broad-sense heritability (h^2).
* $P \leq 0.05$, ** $P \leq 0.01$.

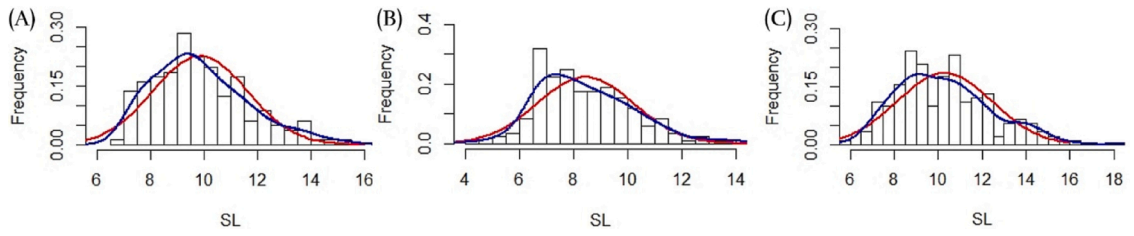

Fig. 1. Frequency distributions of the maize shank length (SL) in three RIL populations in different environments. The blue line represents the frequency distribution curve of SL, whereas the red line represents the standard normal distribution curve. (**A**) BYD population; (**B**) BYK population; (**C**) CIK population.

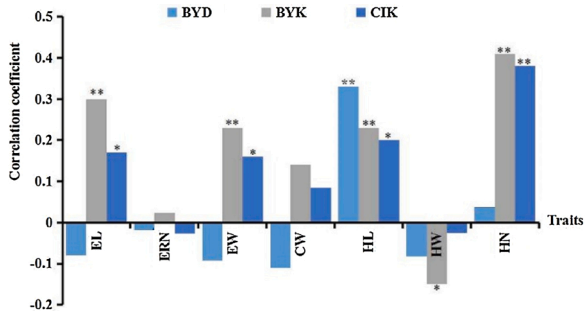

Fig. 2. Correlation between shank length (SL) and four ear traits and three husk traits based on BLUP values in different populations. EL, ear length; ERN, ear row number; EW, ear weight; CW, cob weight; HL, husk length; HW, husk width; HN, husk number. * $P \leq 0.05$; ** $P \leq 0.01$.

were narrowed to peak bins. The physical distances of the peak bins ranged from 0.09 Mb to 0.35 Mb (Table 3), with the peak bins for qSL BYK-2−1, qSL CIK-2−1, qSL CIK-9−1, and qSL CIK-9−2 comprising 2, 5, 6, and 12 protein-coding genes, respectively, according to the MaizeGDB annotated gene database (www.maizegdb.org) (Table 3, Fig. 4). Of these 25 genes, 10 were not annotated, whereas 15 were annotated according to their homologs in *A. thaliana* and rice (Table 3). Moreover, *GRMZM2G168474*, *GRMZM2G172795*, *GRMZM2G066784*, and *GRMZM2G144985* were considered to be candidate genes for SL because of their contributions to the hormone synthesis, transport, and signal transduction that helps regulate cell elongation, division, and differentiation. Another candidate gene for SL, *GRMZM2G101062*, is involved in the sphingolipid biosynthesis that regulates cell expansion.

4. Discussion

4.1. Genetic component of SL in maize

The SL in the three RIL populations examined in this study varied considerably, with a normal distribution. The genetic analysis indicated SL is highly heritable in the three RIL populations. The SL was mainly controlled by three, three, and four QTL with large-effects and small-effects (6.15 %–16.7 %) in the BYD, BYK, and CIK RIL populations, respectively (Table 2). Therefore, our results suggest SL is a polygenic trait controlled by multiple genes with small effects. Interestingly, none of the QTL were common to all three RIL populations, reflecting the complexity of the SL regulation in diverse maize populations. A similar complexity has been revealed for PH. Although many QTL for PH have been identified in various populations, only some are consistent across diverse genetic backgrounds [28,15]. Furthermore, there was a lack of QTL associated with both SL and PH (Fig. S2), indicative of the differences in the genetic regulation of these two traits. Details regarding the QTL for PH in the same populations were derived from a study by Pan et al. [36].

According to the Beavis effect, the small-effect QTL associated with SL are very likely overestimated when there are fewer than 500 progenies [44]. Thus, the maize SL should be further analyzed to preferentially select large-effect QTL. Regarding the small-effect QTL for SL, a meta-analysis of the SL from additional experiments may eliminate the bias related to the Beavis effect [45].

4.2. Relationship between the SL and ear and husk development

In maize, the shank is a lateral organ from which the ear and husk grow. Thus, we investigated the relationship between the shank and the ear and husk. The SL was positively correlated with EL and EW, implying

Table 2
Individual QTL for shank length in three RIL populations.

Populations	QTL	Chromosome	Peak (cM) [a]	Physical Position (Mb) [b]	Genetic interval (cM)	Additive effect [c]	LOD value	Phenotypic variation% [d]
BY815/DE3	qSL BYD-1−1	1	12.4	3.2−4.6	7.7−14.5	−0.57	3.45	6.15
	qSL BYD-2−1	2	91.5	148.7−161.3	89.6−92.9	−0.67	4.60	8.42
	qSL BYD-2−2	2	99.1	170.9−175.5	97.9−100.9	−0.71	5.12	9.31
	Total [e]							13.67
BY815/K22	qSL BYK-2−1	2	77.5	23.0−42.0	67.2−78.4	−0.80	8.34	16.7
	qSL BYK-2−2	2	87.2	64.0−119.5	84.2−87.9	−0.74	6.85	14.5
	qSL BYK-4−1	4	22.7	3.1−5.5	13.2−25.3	−0.56	4.37	8.47
	Total [e]							20.45
CI7/K22	qSL CIK-1−1	1	251.1	293.5−296.8	248.2−252.8	−0.54	4.67	8.00
	qSL CIK-2−1	2	59.2	17.7−20.8	56.5−66.5	−0.65	6.31	11.20
	qSL CIK-9−1	9	79.9	134.0−135.9	79.3−80.5	0.70	7.67	13.38
	qSL CIK-9−2	9	89.3	141.7−142.6	88.1−89.8	0.62	5.78	10.35
	Total [e]							30.81

[a] Peak position (in centimorgans, cM) with the highest logarithm of the odds (LOD) for each QTL.
[b] Physical positions of the identified QTL are based on the B73 reference sequence (version 2) (www.maizesequence.org).
[c] Additive effect (A) of the identified QTL: a positive value indicates that the allele from the female parent increased the shank length, whereas a negative value indicates that the allele from the male parent increased the shank length.
[d] Percentage of the phenotypic variation explained by the additive effect of the identified QTL.
[e] Total percentage of the phenotypic variation explained by all QTL determined by multiple interval mapping.

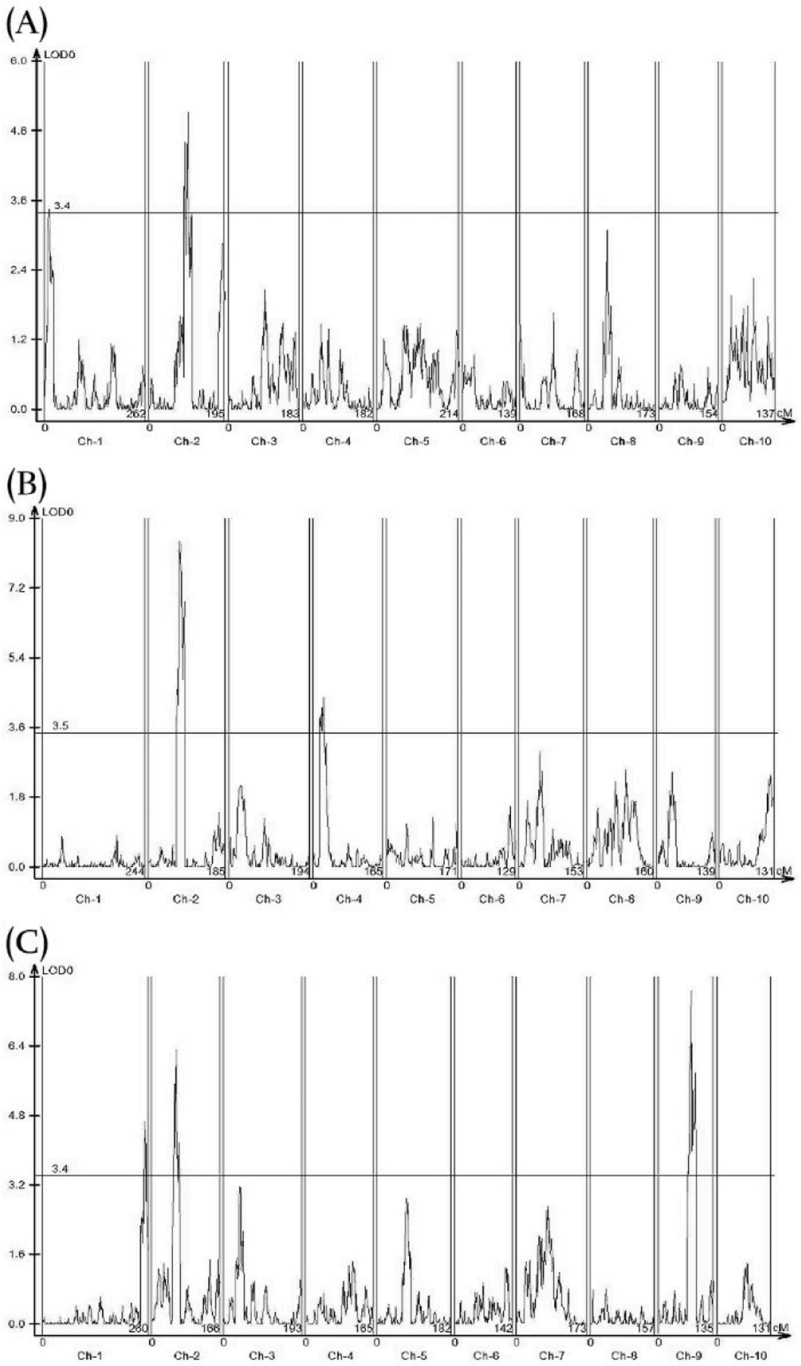

Fig. 3. Logarithm of the odds (LOD) profiles of the identified QTL for maize shank length (SL) in three RIL populations with the best linear unbiased prediction (BLUP) values. (**A**) BYD population; (**B**) BYK population; (**C**) CIK population.

the shank (i.e., length) and ear (i.e., length and weight) develop in a coordinated manner, which influences the grain yield. There was a significant positive correlation between SL and HL, suggesting that long shanks are enclosed by a long husk to prevent the top of the ear from being exposed, thereby increasing the resistance of the ear to pests and diseases. Additionally, as predicted, SL and HN were positively correlated. An earlier study confirmed that the SL is affected by the internode length and the number of nodes, and each node is covered with a layer of husk [46]. Accordingly, our results indirectly prove that the SL partly depends on the number of nodes. Moreover, the genetic overlap of QTL for SL and QTL for four ear traits and three husk traits was analyzed because of the relationships among these traits. Information regarding the QTL related to the ear and husk traits was obtained from previous studies by Xiao [31] and Cui [43], respectively. Our analyses uncovered one genetic overlap between SL and EL on chromosome 1, one genetic overlap between SL and ERN on chromosome 2, two genetic overlaps between SL and CW on chromosome 2, and one genetic overlap between SL and HN on chromosome 2 (Fig. S2). Thus, breeding maize varieties with an ideal SL may enhance husk and ear traits to some extent, which will hopefully increase the maize grain yield and improve mechanical harvesting.

4.3. Putative genes and pathways affecting SL

The size of QTL intervals is influenced by the size of the mapping population as well as marker density. Because high-density SNP bin

Table 3
Genes within the genomic region spanning the single bin for the large-effect QTL peak.

QTL	Chr	Bin at the peak	Bin length (bp)	Number of genes	Gene ID	Gene position(bp)[a]	Annotation[b]
qSL BYK-2−1	2	PZE-102061537	110,033	2	GRMZM5G804251	39953659..39955587	Unknown
					GRMZM2G022637	40003868..40004708	Heavy metal transport/detoxification superfamily protein
qSL CIK-2−1	2	PZE-102038265	93,796	5	GRMZM2G172795	18417370..18421827	Basic helix-loop-helix (bHLH) DNA-binding superfamily protein
					GRMZM2G168474	18460858..18463365	Cis-zeatin O-glucosyltransferase1
					GRMZM2G168516	18466456..18467459	Unknown
					GRMZM2G399862	18507575..18508504	Unknown
					GRMZM2G099130	18509782..18514307	SPT2 chromatin protein
qSL CIK-9−1	9	PZE-109086063	154,772	6	GRMZM2G066784	134609802..134612083	Cytochrome P450 family 721 subfamily A polypeptide 1 (CYP721A1)
					AC206265.3_FG006	134616000..134616651	Unknown
					GRMZM2G358238	134641015..134643501	High chlorophyll fluorescence 243 (HCF243)
					GRMZM2G033846	134720446..134721336	Ca^{2+}-binding protein 1
					GRMZM2G024996	134749957..134751048	Unknown
					GRMZM2G172099	134769888..134772063	GDSL-like Lipase/Acylhydrolase superfamily protein
qSL CIK-9−2	9	PUT-163a-148928873−366	354,807	12	GRMZM2G144985	142289400..142294418	Long-chain base1 (LCB1)
					GRMZM2G145085	142296738..142301939	RNA polymerase II transcription factors (RAP74)
					GRMZM2G700052	142309806..142331129	Unknown
					GRMZM2G104418	142331593..142334452	Vacuolar proton ATPase A2 (VHA-A2)
					GRMZM2G017678	142397242..142399285	UDP-D-glucuronate 4-epimerase 2 (GAE2)
					GRMZM5G828123	142442862..142443440	Unknown
					GRMZM2G101062	142462797..142466161	Abscisic acid-responsive family protein (TB2/DP1 HVA22)
					GRMZM2G101001	142467307..142472205	Unknown
					GRMZM2G100988	142472715..142473732	Unknown
					GRMZM2G067303	142495359..142498679	Ribosomal protein S10p/S20e family protein
					GRMZM2G090792	142619258..142621497	Unknown
					GRMZM2G090842	142642524..142645730	ACT domain repeat 8 (ACR8)

[a] Position according to the B73 reference sequence (version 2).
[b] Name of the homologous gene in *Arabidopsis thaliana* or rice.

maps are useful for efficiently narrowing the QTL interval, it they have been used to study many plant species, including rice, soybean, and maize [24,27,47,48]. In the current study, four large-effect QTL for SL were narrowed from the original 0.9–19.0 Mb interval to a 0.09–0.35 Mb region based on a bin map (Table 3). The small peak bins facilitated the identification of candidate genes, which may be related to PH because the SL is influenced by internode length and node number, as is PH [49,50]. Internode length is related to cell elongation and division, among other factors, whereas node number is related to cell differentiation [51]. These processes are substantially affected by hormone synthesis, transport, and signal transduction [52–55]. Two functionally redundant oxo-phytodienoate reductase genes, *OPR7* and *OPR8*, contribute to JA biosynthesis. Additionally, the *opr7/opr8* double mutant exhibits significant developmental defects, including the extreme elongation of ear shanks and the initiation of female reproductive buds at each node; however, the abnormal development of the mutant can be rescued via the application of exogenous JA. These results indicate that JA is an important factor controlling the maize SL [10]. In the current study, we detected 25 genes inside four peak bins, including five candidate genes correlated with SL in three bins (Table 3). Their association with SL should be further verified via backcrosses and the production of candidate gene knockout or overexpressing mutants.

Regarding qSL BYK-2−1, the interval was narrowed to a 0.11 Mb region with one functionally annotated protein-coding gene (Table 3). Specifically, *GRMZM2G022637* encodes a heavy metal transport/detoxification superfamily protein. An earlier study proved that heavy metal transport/detoxification superfamily proteins are responsive to Cd stress and can transport and detoxify heavy metal ions [56]. However, how *GRMZM2G022637* regulates SL remains unknown, but its effect on SL may be mediated through an unknown pathway.

The qSL CIK-2−1 interval, which was decreased to 0.09 Mb, contains three functionally annotated protein-coding genes (Table 3). Both *GRMZM2G168474* and *GRMZM2G172795* are likely candidate genes for SL because of their functions. *GRMZM2G168474* is a cytokinin-related gene that encodes cis-zeatin O-glucosyltransferase 1 (CZOG1), which binds specifically to cis-zeatin. Previous research indicated that *CZOG1* regulates cis-zeatin levels and is expressed in the roots, stems, and leaves, but some of the specialized functions of *CZOG1* remain uncharacterized in maize [57]. An earlier study on rice demonstrated that mutant lines overexpressing *CZOG1* and *CZOG2* have short shoots and fewer crown roots than the wild-type plants [58]. These phenotypes are consistent with those observed in a previous examination of cytokinin mutants [59]. Therefore, we speculate that *CZOG1* may regulate maize SL by controlling cis-zeatin levels. The *GRMZM2G172795* encodes a bHLH DNA-binding protein involved in auxin signal transduction, which regulates plant growth and development. In *A. thaliana*, ARF3 interacts with bHLH transcription factors to form a dimer that affects the regulatory activity of ARF3 associated with the transcription of downstream auxin-responsive genes; however, the specific target genes need to be further studied [60]. This auxin signal transduction mechanism is necessary for plant organ morphogenesis. Consequently, *GRMZM2G172795* may regulate SL by modulating auxin signal transduction.

The qSL CIK-9−1 interval was narrowed to 0.15 Mb, with four functionally annotated protein-coding genes (Table 3). These genes included *GRMZM2G066784*, which encodes cytochrome P450 family 721 subfamily A polypeptide 1 (CYP721A1). Cytochrome P450 is a broad-spectrum biocatalytic enzyme involved in diverse metabolic processes, including plant hormone biosynthesis and degradation [61]. For example, in *A. thaliana*, CYP735A1 and CYP735A2 catalyze the biosynthesis of trans-zeatin, which is one of the most common active cytokinins in higher plants [62]. The *CYP707* encodes 8′-abscisic acid

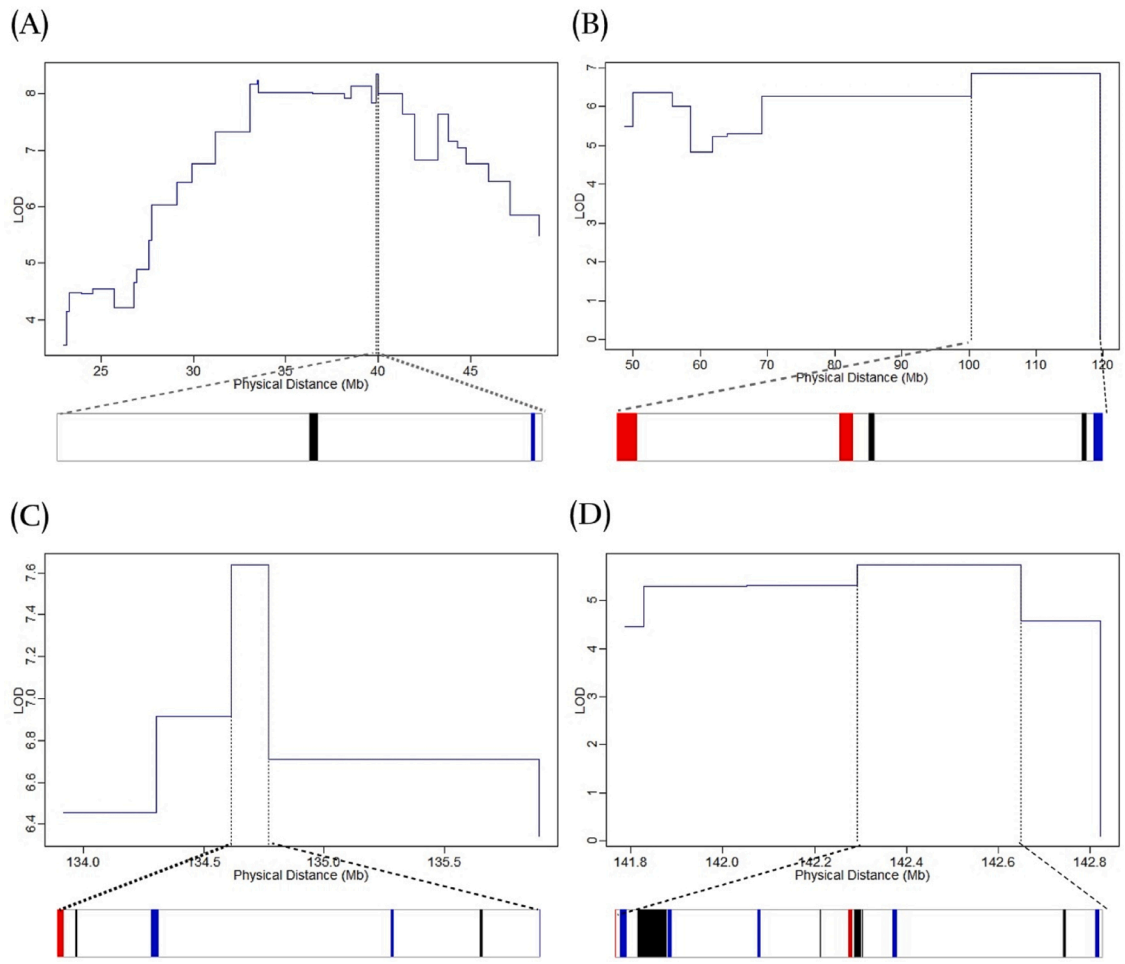

Fig. 4. Logarithm of the odds (LOD) profiles for quantitative trait locus (QTL) bins as well as the locations of the genes in peak bins. The candidate genes for shank length are indicated by red bands. The annotated genes in the peak bin are indicated by blue bands. Other genes in the peak bin are indicated by black bands. (**A**) qSL BYK-2-1; (**B**) qSL CIK-2-1; (**C**) qSL CIK-9-1; (**D**) qSL CIK-9-2.

hydroxylase, which is important for abscisic acid degradation in *A. thaliana* [63]. The *dwarf3* (*d3*) maize mutant exhibits stunted growth, which is due to a defect in an early step of the gibberellic acid biosynthesis pathway. A sequence analysis indicated that the *d3* gene encodes a predicted protein with a sequence that is significantly similar to that of cytochrome P450 enzymes [53]. Therefore, *CYP721A1* may be a candidate gene for SL.

The qSL CIK-9−2 peak bin, which was larger (0.35 Mb) than that of the other four identified large-effect QTL, contains seven functionally annotated protein-coding genes. The *GRMZM2G144985* encodes the long-chain base 1 (LCB1) subunit of serine palmitoyltransferase. The LCB1 and LCB2 subunits combine to form a functional serine palmitoyltransferase complex, which catalyzes the first reaction of the sphingolipid biosynthesis pathway [64]. A mutant in which *LCB1* expression is partially suppressed is reportedly smaller than normal because of restricted cell expansion [65]. In contrast, *GRMZM2G101062* encodes an abscisic acid-responsive family protein (TB2/DP1 HVA22). The abscisic acid-induced accumulation of HVA22 proteins inhibits the vesicular trafficking involved in nutrient mobilization to delay the coalescence of protein storage vacuoles and also helps regulate seed germination and seedling growth [66]. These findings imply that *GRMZM2G144985* and *GRMZM2G101062* may be candidate genes for SL.

According to the data presented herein, most of the candidate genes for SL are associated with the metabolism of hormones, including auxin, cytokinin, and abscisic acid. Additionally, JA, which inhibits plant growth, also adversely affects the maize SL [10]. Increases in auxin contents and decreases in cytokinin and abscisic acid levels promote plant elongation [67,68]. Accordingly, various hormones may cooperatively regulate the SL in maize plants, but this possibility will need to be experimentally verified.

5. Conclusion

A lack of available information regarding the genetic basis and regulatory mechanism responsible for the natural variations in the maize SL compelled us to conduct this in-depth examination of SL. Our results indicate that SL is a quantitative trait that is highly heritable. Moreover, we identified 10 QTL related to SL, five of which were large-effect QTL. In this study, the QTL with the largest effect explained 16.7 % of the SL variation. Five candidate genes for four large-effect QTL were screened. The proteins encoded by these genes may be involved in sphingolipid biosynthesis and the metabolism of plant hormones (e.g., auxin, cytokinin, and abscisic acid). Additionally, SL was revealed to be closely related to ear and husk characteristics, with some genetic overlap in the QTL for these traits. In summary, the identified QTL and candidate genes may be useful for further elucidating the molecular pathways regulating maize SL, with implications for the breeding of new high-yielding maize varieties suitable for mechanical harvesting.

CRediT authorship contribution statement

Meiling Liu: Formal analysis, Software, Writing - original draft, Writing - review & editing, Visualization. **Wenshu He:** Data curation, Investigation. **Ao Zhang:** Supervision. **Lijun Zhang:** Supervision. **Daqiu Sun:** Visualization. **Yuan Gao:** Validation. **Pengzun Ni:** Validation. **Xinglin Ma:** Data curation, Investigation. **Zhenhai Cui:** Conceptualization, Supervision. **Yanye Ruan:** Conceptualization.

Declaration of Competing Interest

Our manuscript has no conflict of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.plantsci.2020.110767.

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